MALE GENITALIA OF SOME CURCULIONOIDEA (COLEOPTERA): MUSCULATURE AND DISCUSSION OF FUNCTION

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ABSTRACT

The male genital complex and associated musculature are described for 5 different species of Curculionoidea.

The genital complex consists of an intromittent organ, the median lobe with its apodemes, the median struts, and a tegmen and spiculum gastrale on which the muscles which protract and retract the median lobe have their origins. Associated with the genital complex are tergum VIII and abdominal sterna VII and VIII on which muscles moving the tegmen and spiculum gastrale have their origins. Modifications in the structure of the spiculum gastrale and its connections to the tegmen are associated with changes in the function of homologous muscles.

INTRODUCTION

The impetus for this study was observation of major differences in the structure of some parts of the male genital complex in 2 groups of weevils in the tribe Tychiini (*sensu* Clark *et al.* (1977)). In order to determine homologies of these parts and to determine which of the different expressions were plesiotypic (primitive) in Tychiini, genitalia of several representatives of the superfamily Curculionoidea were examined. The following 5 species were studied in detail and form the basis of discussion: *Arrhenodes minutus* (Drury) (Brentidae), *Curculio victoriensis* Pierce (Curculionidea: Curculioninae), *Scyphophorus acupunctatus* Gyll. (Curculionidae: Rhynchophorinae), *Tychius tectus* LeConte, and *Sibinia suturalis* (Schaeffer) (Curculionidae: Tychiinae). The first 3 were selected in part because of availability of specimens which could be used for dissection. *Tychius* and *Sibinia* represent 2 major groups in the tribe Tychiini.

In all, the taxa studied represent only 2 of the 9 families of Curculionoidea recognized by Crowson (1967). One of Crowson's families, Curculionidae, includes taxa which many have preferred to recognize as separate families, the Scolytidae and Platypodidae. One author with such preference, Wood (1973), presents evidence which he interprets to indicate the existence of 3 major groups of Curculionoidea: (1) taxa with 2 gular sutures, entire or incomplete (Belidae, Anthribidae, Nemonychidae, Oxycorynidae, and Proterhinidae); (2) those with 1 gular suture but with pregular sutures (Scolytidae and Platypodidae); and (3) those with 1 gular suture and no pregular sutures (Brentidae, and Crowson's Apionidae, Attelabidae, and Curculionidae). The taxa examined in the present study all belong to the 3rd group. These have been compared, however, with published descriptions and illustrations of members of the 2nd group. More representatives of the 3rd group, as well as members of the 1st group, need to be examined and

compared with members of the 2nd group and with each other, with the objective of recognition of synapomorphies within the entire superfamily. This is beyond the scope of my initial objective, and no hypotheses about phylogenetic relationships of major taxa within Curculionoidea are proposed here. Interpretation of my observations as related to phylogeny within the tribe Tychiini will be discussed in a paper dealing with the phylogeny and classification of species of the genus *Sibinia* (in preparation).

Literature pertaining to the male genital complex of Coleoptera is not extensive. Hieke (1966) presents the most comprehensive bibliography on the subject that I have seen. Several workers have dealt primarily with Curculionoidea, or have included representatives of the group in their studies. I have compared my observations with those made by Burke (1959), *Anthonomus grandis* Boh. (Curculionidae: Anthonominae); Muir (1919), *Rhynchophorus ferruginous* (Curculionidae: Rhynchophorinae); Hieke (1966) *Liparus glabrirostris* Kust., (Curculionidae: Hylobiinae); Hopkins (1911) *Pissodes* sp. (Curculionidae: Pissodinae) and (1915) *Dendroctonus valens* LeConte (Scolytidae) and *Crossotarsus lecontei* (Platypodidae). Reference to these genera in the following discussion is to these sources rather than direct observations by me. I also consulted the works of Kingsolver (1970) on Bruchidae, Evans (1961) on Cryptophagidae, and Pu (1938) on several families, particularly Cerambycidae, in an attempt to determine homologies of muscles. Probable homology of muscle bands is listed in Table 1.

Terminology is that of Sharp & Muir (1912) which, as Kingsolver (1970) pointed out, is more widely accepted among coleopterists than other systems which have been proposed. Tuxen's (1970) glossary may be consulted to determine correlations with other terminologies. Muscle bands are herein designated by numbers which correspond to those used by Burke (1959). Other workers have referred to muscle bands by names denoting their functions. This would lead to confusion in the present paper as some homologous muscle bands have different functions in different Curculionoidea.

Genital preparations were made by dissecting some specimens preserved in 70% ethyl alcohol, some pinned specimens, and some fresh specimens treated with a solution developed by Weaver and Thomas (1956). Specimens preserved in alcohol proved to be most satisfactory for study of musculature. Dry specimens were softened in hot water. When only sclerotized parts were desired a hot potassium hydroxide solution was used to dissolve soft tissue. All observations and drawings were made of specimens immersed in glycerin.

Abbreviations used in figures 1-15 are: genital muscles 1-10 (GM-1-10); basal piece of tegmen (bpt); lateral lobes of tegmen (ll); median lobe (ml); median struts (ms); pseudo-tegmen (pt); spiculum gastrale (sg); sternum 8 (SVIII); tegmen (t); tegminal strut (ts); tergum 8 (TVIII).

General Morphology

A brief description of the sclerotized and membranous structures of the genital complex and a discussion of some of their modifications is essential to an understanding of their functions and relationships. For a more detailed description see Burke (1959) and Sharp (1918). Only those structures and muscles involved in protrusion and retraction of the median lobe were studied.

Table I

Probable Muscle Homologies

| Clark	Burke	Hieke	Muir	Hopkins	Kingsolver	Pu	Evans
GM-1	GM-1	M.Phb.ph.ap.	d	el	MLV(pars)	47	PEP
GM-2	GM-2	M.Phb.ph.ap.?	absent	el	MLV(Pars)	54	isc
GM-3	GM-3	M.phb.endoph.	c	e2	MLV(pars)	48	PER
GM-4	GM-4	M.terg.ap.phb.(pars)	--	--	tr	52	TER
GM-5	GM-5	M.terg.ap.phb.(pars)	--	--	tr?	52?	TED
GM-6	GM-6	M.Urost.phb.	b	e3	tp	50	tepa
GM-7	GM-7	M.antec.uron.lat.VIII	a(pars)	--	sds	57?	ssp
GM-8	GM-8	M.antec.uron-medVIII	a(pars)	--	sps	57?	ssd
GM-9	--	M.antec.Urost.VIII	a(pars)	e3	svs	55or56	ssv
GM-10	--	M.Urost.terg.ap.	--	--	--	55?	tsp

The male intromittent organ in Curculionoidea is called the median lobe (ml, Figs. 6, 7, 9, 11, 13, 14, 15). It is composed of a more or less flattened and curved tube with a pair of elongate, laterobasal apodemes called the median struts (ms, Figs. 6, 8, 11, 13, 14, 15) which project anteriorly into the abdomen. In its resting position the median lobe lies in the abdomen horizontal to the long axis of the body. Its structure is essentially the same in all of the forms observed except in Platypodidae in which there are no true struts (Sharp 1918).

Muscle bands involved in protraction and retraction of the median lobe insert on the tegmen and on the spiculum gastrale. The tegmen consists of a basal piece (bpt, Fig. 10) which lies ventral to the median lobe and forms a complete or partial ring through which the median lobe passes, and a pair of lateral lobes (ll, Fig. 7) which arise on the dorsal portion of the ring and extend posteriorly in the body dorsal and lateral to the median lobe. The basal piece usually has a ventral apodeme, the tegminal strut (ts, Fig. 7). In Curculionoidea, the lateral lobes are often absent and the ring formed by the basal piece may be membranous dorsally (see Morimoto 1962 and Clark et al. 1977). In *Curculio* and *Scyphophorus* the basal piece forms a nearly complete sclerotized ring. Lateral lobes are present in *Arrhenodes* and *Anthonomus*. In *Tychius, Sibinia,* and *Crossotarsus,* the basal piece and tegminal strut form a distinct Y-shaped structure which lies ventral to the median lobe. The arms of the Y are connected by membrane forming a ring through which the median lobe passes. The tegminal strut is very short in *Liparus* and absent in *Dendroctonus.* Only the basal piece and its strut are involved in muscle attachment.

Some significant modifications were noted in the structure of the spiculum gastrale (sg, Figs. 6, 7, 9, 10, 11, 14, 15). This structure is usually considered to be a remnant of the 9th abdominal sternum in Coleoptera, although some studies do not bear this out. Evans (1961) discussed the evidence and cited pertinent references.

In most Curculionoidea the spiculum gastrale has a broad basal sclerotized portion which is continuous with the first connecting membrane, and a prominent sclerotized rod which projects anteriorly in the body. This type of structure was illustrated by Burke (1959) for *Anthonomus,* Schoof (1942) for *Conotrachelus,* Hieke (1966) for *Liparus,* and Jeannel and Paulian (1944) for *Ectomnorrhipus* and *Phyllobius,* and is also present in the brentid, *Arrhenodes* (Fig. 1). I observed a similar type of spiculum gastrale in the curculionid subfamilies Brachyrrhininae, Thylacitinae, Tanymecinae, Leptopiinae, Cylindrorhininae, Hylobiinae, Erirhininae, Apioninae, Rhynchitinae, Pterocolinae, Myrmecinae, Anthonominae, Rhynchaeninae, Cryptorohynchinae, Ceutorynchinae, and Baridinae. The basal portion may be very lightly sclerotized and often the edges are difficult to distinguish from the membrane with which they are continuous. In *Pissodes* (Pissodinae) (Hopkins 1911) and *Lixus* (Cleoninae) (Morimoto 1962) the basal portion is apparently completely membranous, and only the rod is discernible.

In *Curculio* the rod of the spiculum gastrale appears to arise directly from the first connecting membrane (Fig. 2). Lying in the membrane on each side of the base of the rod are 2 sclerotized pieces which Bissell (1937) called "spicule plates". Gilbert (1952) described what he called spicule plates in
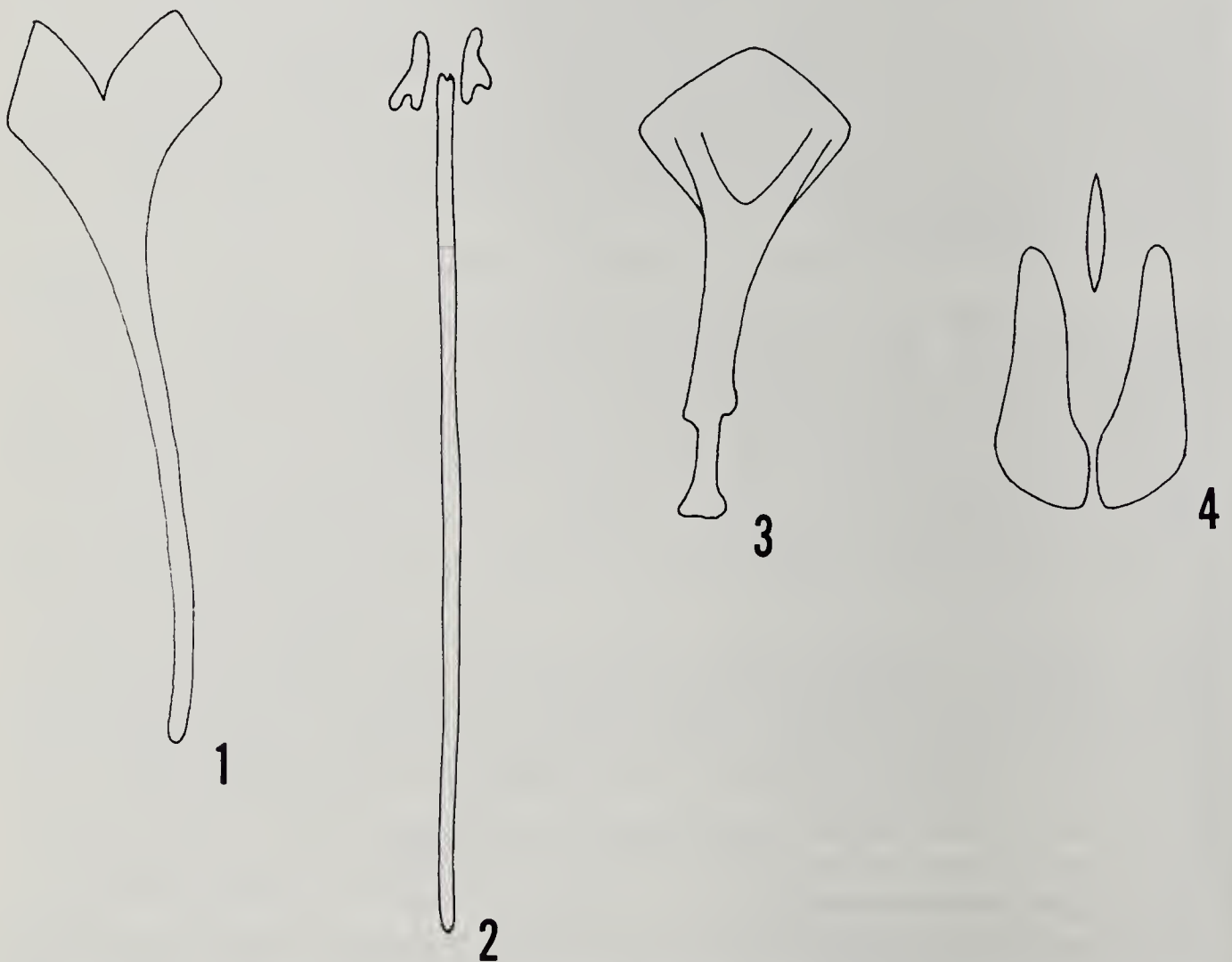
Figs. 1-4, ventral views of spiculi gastrale of: 1) *Arrhenodes minuta* (Drury) (Brentidae); 2) *Curculio victoriensis* Pierce (Curculioninae); 3) *Tychius tectus* LeConte (Tychiinae); 4) *Sibinia suturalis* (Schaeffer) (Tychiinae).

the trogositid *Temnochila* and in the curculionids *Eugnamptus* (Eugnamptinae) and *Cossonus* (Cossoninae); these sclerites are connected to the spiculum gastrale in *Cossonus*. In the specimens of *Eugnamptus* that I examined there is a large sclerotized area continuous with the first connecting membrane which lies between the basal portion of the spiculum gastrale and sternum VIII but which is not attached to either. I observed a similar but much smaller sclerite in *Arrhenodes*. No muscles attach to these sclerites and it is doubtful that they are homologous to Bissel's (1937) "spicule plates" of *Curculio*. Conversely, muscles attached to these "spicule plates" are homologous to the muscles attached to the basal portion of the spiculum gastrale in the other forms studied. The "spicule plates" in *Curculio* then should be considered homologous to the basal portion of the spiculum gastrale and not to the "spicule plates" described by Gilbert in *Temnochila, Eugnamptus,* and *Cossonus*.

In Rhynchophorinae, the first connecting membrane forms an expanded rigid opaque tube which Sharp (1918) called the pseudo-tegmen (pt, figs. 10-13). In *Scyphophorus* the rod of the spiculum gastrale arises in the medioventral portion of the pseudo-tegmen (Fig. 11). Muscles whose homologs attach to the basal portion of the spiculum gastrale in most other Curculionoidea are attached to the lateral and ventral surfaces of the pseudo-tegmen in *Scyphophorus*. The spiculum gastrale is absent in some Rhynchophorinae (Sharp 1918).

In *Tychius,* the rod of the spiculum gastrale diverges at its base to form a Y-shaped structure (Fig. 3). The arms of the Y are simply thickened portions of a large basal sclerotized plate. The rod is comparatively short and the apex bears knobs which increase area for muscle attachment.

In *Sibinia* the rod of the spiculum gastrale is absent (Fig. 4). The basal portion is modified to consist of 3 separate sclerotized plates, 2 large anterolateral plates and a small posteromedian plate. The muscles attached to these plates are homologous to those arising on the basal portion of the spiculum gastrale in those Curculionoidea which do have a spiculum rod. The anterolateral plates are firmly attached posteriorly to the basal piece of the tegmen by a short stiff membrane so that the 2 structures function as an inflexible unit instead of independently.

MUSCULATURE OF THE GENITAL COMPLEX

Ten muscle bands are directly or indirectly involved with protraction and retraction of the median lobe. These bands have their origins and insertions on the tegmen, spiculum gastrale, median struts, tergum VIII, and sternum VII or VIII. Since some homologous bands have different functions and/or points of origin or insertion, they are here designated by numbers. Table 1 lists probable homology of muscles described here and those described by other workers.

Genital Muscle Number 1 (GM-1)

GM-1 is the protractor of the median lobe. It may consist of a pair of bands or a single band and is present in all of the forms studied. The origin is on the basal piece of the tegmen, the insertion on the apical portions of the median struts. Upon contraction of GM-1 the median lobe is moved posteriorly.

In *Arrhenodes, Curculio, Tychius, Scyphophorus, Crossotarsus,* and *Anthonomus* 2 separate and distinct bands can be discerned. In *Curculio* (Fig. 8), *Scyphophorus* (Fig. 10), and *Anthonomus* these originate on the ventral and lateral margins of the basal piece of the tegmen. In *Arrhenodes* (Figs. 5 and 7), *Tychius* (Fig. 14) and *Crossotarsus,* the origin is on the points of the arms of the Y-shaped tegmen.

In *Sibinia* and *Liparus,* GM-1 is a single, broad band. In *Sibinia* (Fig. 15) its origin is dorsal to the median lobe on the dorsal membranous portion of the ring formed by the basal piece of the tegmen.

In *Arrhenodes* (Figs. 5 and 7) the insertion is on the ventral surface of the flattened apices of the median struts. In all other forms examined (Figs. 8, 10, and 15) the insertion is along the sides of the apices of the median struts.

Genital Muscle Number 2 (GM-2)

In most curculionoids studied GM-2 is a protractor of the median lobe. It consists of a pair of bands in all forms studied. The origin is on the apex of the tegminal strut and the insertion on the inner, or in *Arrhenodes,* on the ventral surfaces of the median struts (Figs. 6, 7, 8, 12, and 14). In *Dendroctonus* the tegminal strut is absent and in *Liparus* it is very short. In these GM-1 and GM-2 are indistinguishable. No trace of GM-2 could be found in *Sibinia.*

In *Scyphophorus* (Fig. 12) the tegminal strut is very long and in that genus GM-2 must act as a retractor of the median lobe.
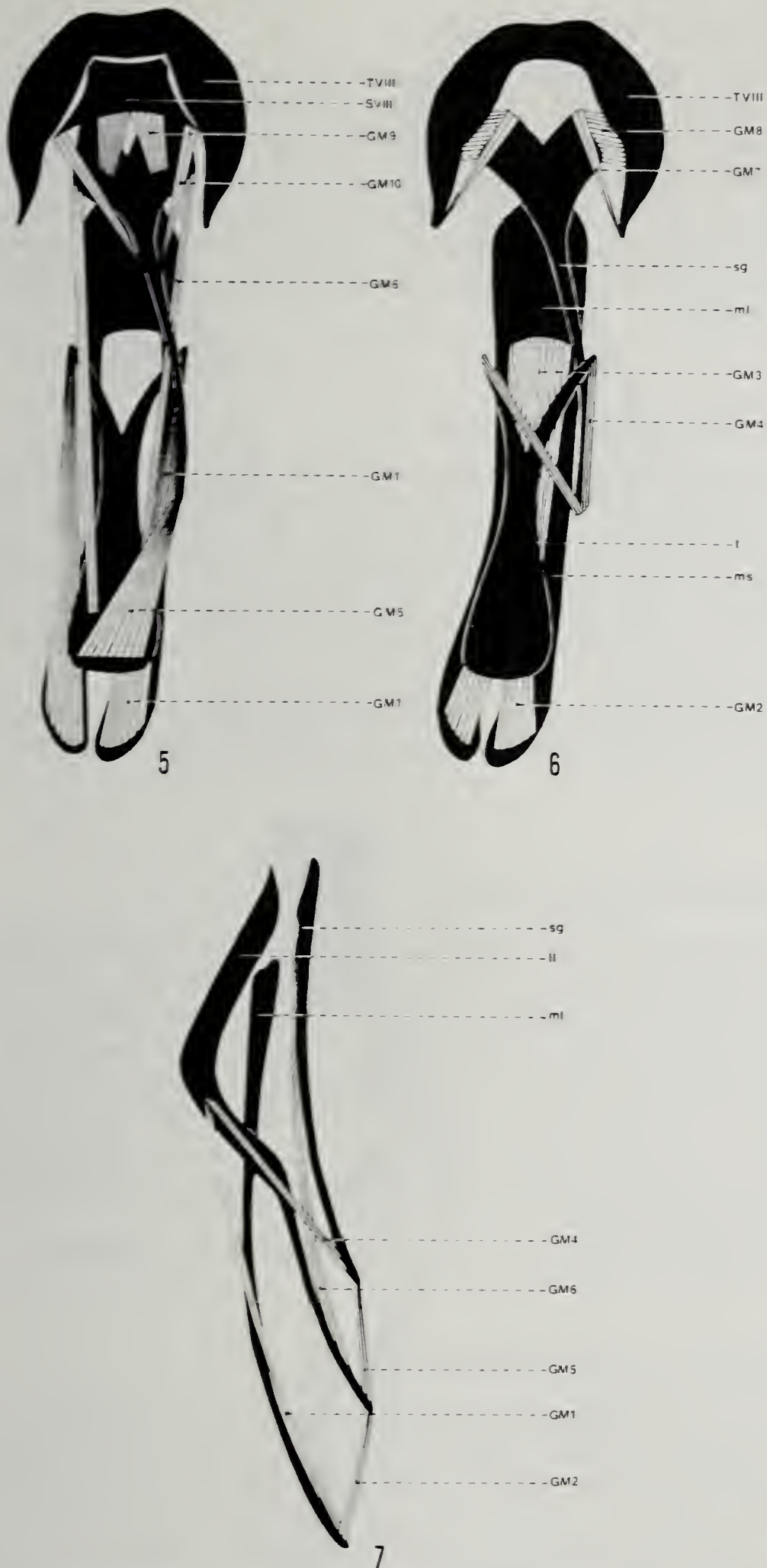
Genital Muscle Number 3 (GM-3)

GM-3 is a retractor of the median lobe. Its origin is on the apical portion of the tegminal strut except in *Dendroctonus* where it is on the apex of the rod of the spiculum gastrale. In *Arrhenodes* (Figs. 6 and 7), *Anthonomus,* and *Sibinia* (Fig. 15) GM-3 consists of a single band inserting along the apicoventral margin of the median lobe. In *Curculio* (Fig. 9), and *Tychius* it is composed of a pair of bands inserting laterally on the apicoventral margin of the median lobe, in *Scyphophorus* (Fig. 13) on the bases of the median struts themselves.

Genital Muscle Number 4 (GM-4)

In *Arrhenodes* (Figs. 6 and 7), *Curculio* (Fig. 9), *Scyphophorus* (Fig. 12), *Liparus,* and *Anthonomus,* GM-4 functions as a retractor of the tegmen. In *Tychius* (Fig. 14) it binds the tegmen and spiculum gastrale together so that they move together as a single unit. GM-4 is absent in *Sibinia* where the spiculum gastrale and tegmen are fused into a single unit retracted by GM-7 and GM-8. Hopkins did not illustrate comparable bands in *Dendroctonus* or *Crossotarsus.*

The origin of GM-4 is on the extreme apex of the rod of the spiculum gastrale, the insertion on the basal piece of the tegmen. In *Scyphophorus* the insertion is on the lateral surfaces and in *Curculio, Liparus,* and *Anthonomus* on the left ventral and lateral surfaces of the basal piece of the tegmen. In *Arrhenodes* and *Tychius* the insertion is on the points of the arms of the Y-shaped tegmen.

Figs. 5-7, male genital complex of *Arrhenodes minuta* (Drury): 5) ventral view showing protractor muscles; 6) ventral view showing retractor muscles; 7) lateral view showing protractor and retractor muscles.

Genital Muscle Number 5 (GM-5)

According to Burke (1959) this band is a retractor of the tegmen in *Anthonomus*. In *Arrhenodes* (Figs. 5 and 7) GM-5 cannot function as a retractor because of the position of the tegmen in relation to the spiculum gastrale when the later is contracted, and must serve mainly to stabilize the apex of the rod of the spiculum gastrale. GM-5 may be homologous to part of GM-4 in *Tychius* and *Liparus*. It was not observed in *Scyphophorus, Sibinia,* and *Curculio* and was not illustrated by Hopkins in *Dendroctonus* or *Crossotarsus*.

Genital Muscle Number 6 (GM-6)

GM-6 is a protractor of the tegmen. When present it consists of a pair of bands. In *Arrhenodes* (Figs. 5 and 7), *Curculio* (Fig. 8), *Anthonomus,* and *Liparus,* the origin is on the anterior margin of the basal portion of the spiculum gastrale, the insertion on the ventral and lateral margins of the pseudo-tegmen. In *Dendroctonus* and *Crossotarsus,* according to Hopkins (1915) the origin is on the posterior margin of sternum VIII rather than on the spiculum gastrale.

GM-6 is absent in *Tychius* and *Sibinia.* Protraction of the tegmen is accomplished by the protractors of the spiculum gastrale which are connected to the tegmen.
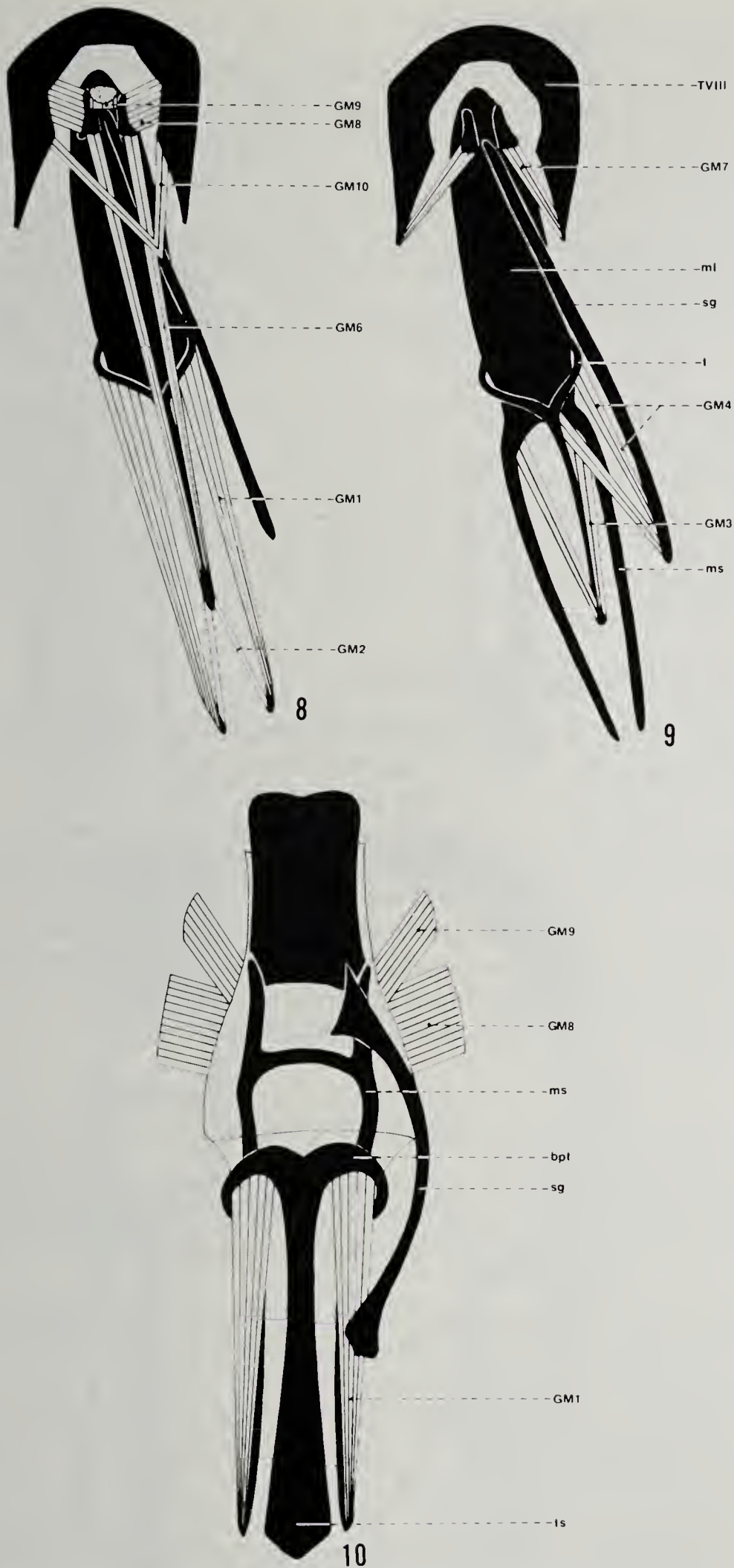
Genital Muscle Number 7 (GM-7)

GM-7 is antagonistic to GM-9 and GM-10. It moves the basal portion of the spiculum gastrale forward in the body. It consists of a pair of bands with origins on the basal apodemes of tergum VIII. The insertion in *Curculio* (Fig. 9), *Anthonomus,* and *Tychius* (Fig. 14) is on the base of the spiculum gastrale in *Arrhenodes* (Fig. 6) on the posterior angles of that structure, in *Scyphophorus* (Fig. 12) on the posterolateral surface of the pseudo-tegmen near the point of attachment of the median lobe and the median struts, and in *Sibinia* (Fig. 15) on the posterior extremes of the anterolateral plates of the spiculum gastrale.

GM-7 is apparently absent in *Dendroctonus* and *Crossotarsus*.

Genital Muscle Number 8 (GM-8)

GM-8 is a suspensor of the basal portion of the spiculum gastrale. It consists of a pair of bands which originate on tergum VIII. Upon contraction of GM-8 the basal portion of the spiculum gastrale is pulled upward and slightly anteriorly toward tergum VIII. The insertion is on the basal portion of the spiculum gastrale on the lateral margin in *Curculio* (Fig. 8), *Tychius* (Fig. 15), and *Anthonomus,* on the posterior angles in *Arrhenodes* (Fig. 6), and on the lateral margins of the anterolateral plates in *Sibinia* (Fig. 15). In *Scyphophorus* (Fig. 10) the insertion is on the lateral surfaces of the pseudo-tegmen slightly anterior to the point of attachment of the spiculum gastrale.

GM-8 is apparently absent in *Dendroctonus* and *Crossotarsus*.

Figs. 8-10, ventral views of male genital complex of: 8) *Curculio victoriensis* Pierce showing protractor muscles; 9) the same showing retractor muscles; 10) *Scyphophorus acupunctatus* Gyll. showing some protractor muscles.

Genital Muscle Number 9 (GM-9)

GM-9 consists of a pair of bands which are antagonistic to GM-7 and GM-8. Its contraction pulls the basal portion of the spiculum gastrale posteriorly and ventrally in the body. It is absent in *Anthonomus* and apparently in *Crossotarsus*.

The origin in *Arrhenodes* (Fig. 5), *Liparus, Curculio* (Fig. 8), *Dendroctonus,* and *Pissodes* is on the anterior margin of sternum VIII, in *Scyphophorus* (Fig. 10) on the dorsomedian surface of that structure. In *Tychius* (Fig. 14) and *Sibinia* (Fig. 15) sternum VIII is reduced to 2 small lateral disc shaped sclerites, and the origin of GM-9 is on the dorsal surface of sternum VII.

The insertion in *Curculio, Liparus,* and *Tychius* is on the dorsomedian surface of the basal portion of the spiculum gastrale, in *Scyphophorus* on the posterolateral surface of the pseudo-tegmen near the point of attachment of the median lobe and median struts. In *Sibinia* 4 distinct bands can be distinguished, 2 of which insert on the posteromedian plate, the other 2 on the inner edge of the posterior portion of the anterolateral plates of the spiculum gastrale.

Genital Muscle Number 10 (GM-10)

GM-10 consists of a pair of bands antagonistic to GM-7. Upon contraction of these bands the spiculum gastrale is moved posteriorly in the body. The origin is on the anterior margin of sternum VIII in *Arrhenodes* (Fig. 5) and on the ventrolateral margin of tergum VIII just anterior to the point of articulation with sternum VIII in *Curculio* (Fig. 8), *Tychius* (Fig. 14), and *Sibinia* (Fig. 15). The insertion is on the rod of the spiculum gastrale in about the basal 1/3 to 1/2 in *Arrhenodes* and on the extreme apex in *Tychius*. In *Sibinia* (Fig. 15) the insertion is on the inner median surface of the anterolateral plates of the spiculum gastrale.

GM-10 is absent in *Anthonomus* and *Scyphophorus*.

PROTRUSION AND RETRACTION OF THE MEDIAN LOBE

This is accomplished by contraction of muscles attached to tergum VIII, sternum VIII or VII, the spiculum gastrale, and the tegmen. The process may be viewed as occurring in 2 steps, each composed of 3 substeps as follows:

Step 1—protrusion of the median lobe—substep 1: protraction of the spiculum gastrale; substep 2: protraction of the tegmen; substep 3: protrusion of the median lobe.

Step 2—retraction of the median lobe—substep 1: retraction of the spiculum gastrale; substep 2: retraction of the tegmen; substep 3: retraction of the median lobe.

In general features, the structure of the genital complex of *Arrhenodes* (Figs. 5-7), *Anthonomus,* and of *Curculio* (Figs. 8 and 9) are the same. In these genera, protrusion and retraction of the median lobe are accomplished as follows. Contraction of GM-8 and GM-10 pulls the basal portion of the spiculum gastrale posteriorly and probably slightly dorsally. With the spiculum gastrale in this position contraction of GM-6 pulls the tegmen posteriorly, bringing GM-1 and GM-2 into position to pull the median lobe posteriorly.
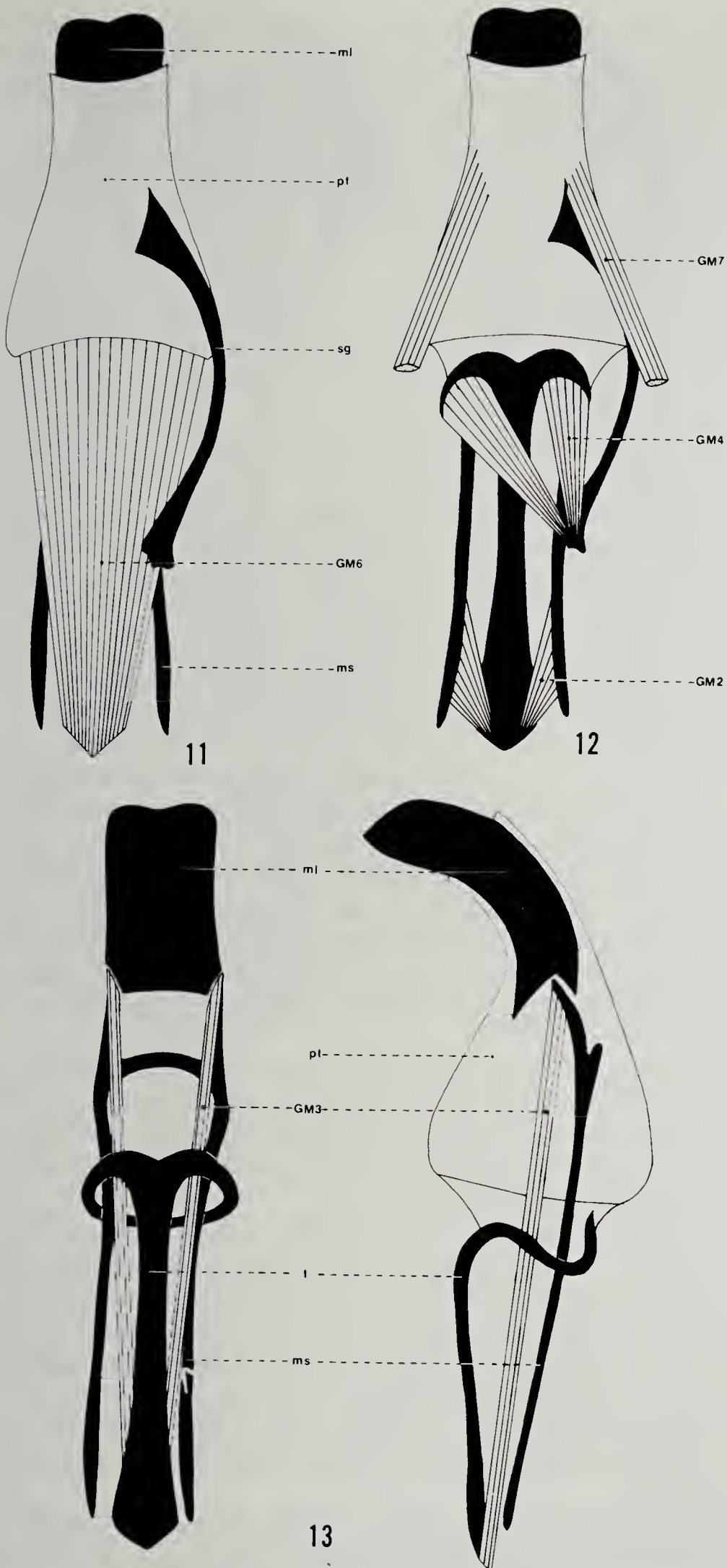
Figs. 11-13, male genital complex of *Scyphophorus acupunctatus* Gyll.: 11) ventral view showing some protractor muscles; 12) ventral view showing some retractor muscles; 13) ventral and lateral views showing some retractor muscles.

The reverse procedure brings the parts back to their resting position; first GM-7 contracts to bring the basal portion of the spiculum gastrale back to its resting position. Acting with GM-7, GM-9 also pulls the spiculum gastrale anteriorly and probably also ventrally.

With the spiculum gastrale restored, the tegmen can be retracted. This is accomplished by contraction of GM-4 which pulls the tegmen anteriorly. Spiculum gastrale and tegmen both restored, contraction of GM-3 pulls the median lobe back into the body.

The same 6 substep sequence occurs in protrusion and retraction of the median lobe in *Scyphophorus* (Figs. 10-13) but here there are structural modifications which give some homologous muscles a different function. The most obvious structural modification in *Scyphophorus* is the thickening and consequent rigidity of the first connecting membrane to form the pseudo-tegmen. Muscles whose homologs attach to the basal portion of the spiculum gastrale in *Arrhenodes* and *Curculio,* are in *Scyphophorus* attached to the pseudo-tegmen, although here they occupy approximately the same position relative to the median lobe and tergum VIII. In *Scyphophorus* GM-10 is absent and GM-9 pulls the pseudo-tegmen and consequently the spiculum gastrale posteriorly instead of anteriorly. The tegminal strut is much longer in relation to the median struts in *Scyphophorus* than in *Arrhenodes* and *Curculio.* In *Scyphophorus* GM-2 is a retractor of the tegmen instead of a protractor of the median lobe.

In *Scyphophorus* protrusion and retraction of the median lobe proceeds as follows. Contraction of GM-9 pulls the pseudo-tegmen posteriorly and probably slightly ventrally. The pseudo-tegmen in contracted position GM-6 pulls the tegmen posteriorly, beneath the anterior margin of the pseudo-tegmen, then contraction of GM-1 protrudes the median lobe.

The first phase of retraction of the median lobe is the contraction of GM-7 and GM-8 which brings the pseudo-tegmen and spiculum gastrale anteriorly to their resting position. Then contraction of GM-4 and GM-2 brings the tegmen forward, and contraction of GM-3 brings the median lobe back into the body.

In *Tychius* (Fig. 14) and *Sibinia* (Fig. 15), the 6 substeps are reduced to 4 because the spiculum gastrale and tegmen are coupled into 1 functional unit. This eliminates the separate substeps necessary for protraction and retraction of the tegmen. Another modification is the shift of the origin of GM-9 from sternum VIII to sternum VII.

Protrusion and retraction of the median lobe in *Tychius* and *Sibinia* is as follows. Contraction of GM-9 and GM-10 pulls the spiculum gastrale posteriorly and ventrally in the body. In *Tychius* GM-4 holds the spiculum gastrale and the tegmen together so that they function as a single unit; in *Sibinia* GM-4 is absent and fusion is accomplished by a membranous connection between the spiculum gastrale and the basal piece of the tegmen. Next in *Tychius,* contraction of GM-1 and GM-2 pulls the median lobe posteriorly and out of the body; in *Sibinia* GM-2 is absent and protrusion is by GM-1 alone.

Retraction of the median lobe is accomplished in 2 steps: contraction of GM-7 and GM-8 pulls the spiculum base and tegmen forward in the body; GM-3 contracts and pulls the median lobe back into the body.

The following discussion of function in *Dendroctonus* and *Crossotarsus* is based solely on Hopkins figures. No direct observations were made.
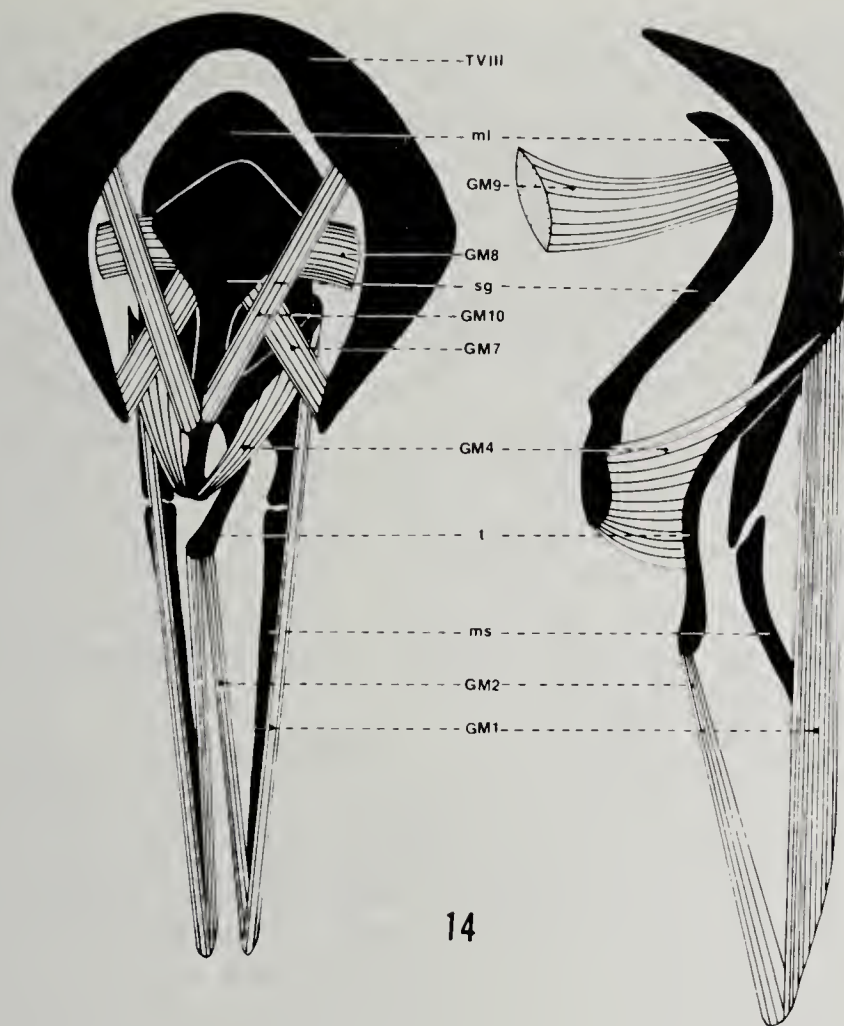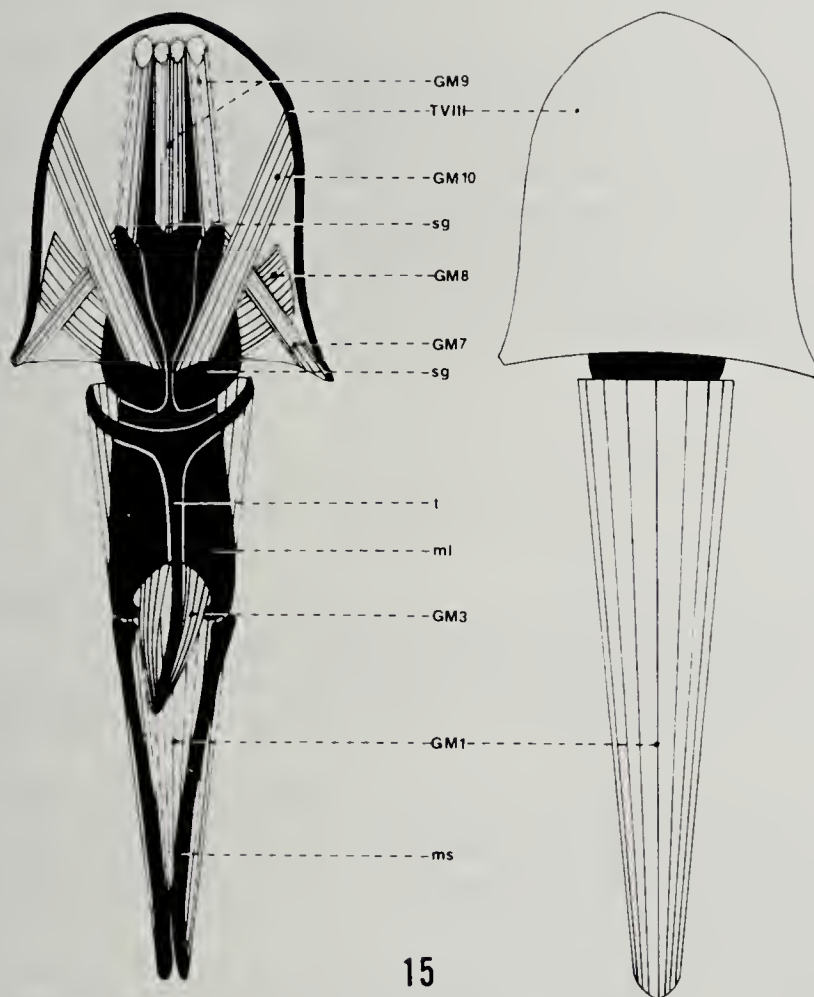
Figs. 14-15, ventral and lateral views of male genital complex of:
14) *Tychius tectus* LeConte showing protractor and retractor muscles;
15) *Sibinia suturalis* (Schaeffer) showing protractor and retractor muscles.

In *Dendroctonus* there are apparently no protractors or retractors of the spiculum gastrale so it must remain stationary during protraction and retraction of the median lobe. Hopkins does not illustrate a retractor of the tegmen either. The following description is therefore tentative.

Step 1, protrusion of the median lobe proceeds as follows: contraction of GM-6 (e3 in Hopkins figure) pulls the tegmen posteriorly; GM-1 (e1) contracts and the median lobe is protruded.

The sequence in step 2 is unclear since no retractor of the tegmen is figured. Evidently the need for substep 1, retraction of the spiculum gastrale, is eliminated because that structure remains stationary. It is possible that part of the large complex band labelled e1, and called the protractor, is actually connected to the apical portion of the spiculum gastrale and acts as a retractor of the tegmen. GM-3 (e2) is attached to the apex of the spiculum gastrale instead of to the apex of the tegminal strut, but its contraction accomplishes the same thing as in the other forms studied, namely retraction of the median lobe.

There is no spiculum gastrale in *Crossotarsus*. The first step, protrusion of the median lobe, proceeds as follows: GM-6 (e3), which originates on sternum VIII and inserts on the tegmen, contracts and pulls the tegmen posteriorly. Protrusion of the median lobe is accomplished by contraction of GM-1 (e1). Again, as in *Dendroctonus*, no retractors of the tegmen are illustrated so it is unclear how this structure is restored to its resting position. GM-3 (e2) is certainly the retractor of the median lobe.

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LITERATURE NOTICE

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